URSPRUNG, H. and R. NÖTHIGER (Editors). 1972. The Biology of Imaginal Disks. Volume 5 *in*: Results and Problems in Cell Differentiation. A series of Topical Volumes in Developmental Biology. Springer-Verlag, New York, Heidelberg, Berlin. xvii + 172 pp., 56 figures, 12 tables. Cloth 8vo $14.60 (U. S.).

This monograph reviews recent research on insect imaginal discs – chiefly those of Diptera-Cyclorrhapha and principally those of *Drosophila* species. The book contains six review articles, each with its own bibliography: (1) R. Nöthiger: The larval development of imaginal discs, (2) W. Gehring: The stability of the determined state in cultures of imaginal discs in *Drosophila*, (3) A. García-Bellido: Pattern formation in imaginal discs, (4) H. Ursprung: The fine structure of imaginal discs, (5) J. W. Fristrom: The biochemistry of imaginal disc development and (6) H. Oberlander: The hormonal control of development of imaginal discs. Although each article stands alone, there is considerable overlap, particularly in the first three contributions. All of the authors are productive contributors to the subject reviewed and are former students or associates of Ernst Hadorn, the Swiss embryologist who first realized the heuristic value of imaginal discs and to whom the book is dedicated. D. Bodenstein, in a eulogy recognizing Hadorn's 70th birthday, summarizes his contributions at the beginning of the book. A fuller account together with lists of his publications and theses done under his direction can be found in Chen, P. S., P. Tardent and H. Burla. 1971. Ernst Hadorn zum siebzigsten Geburtstag. Revue Suisse de Zoologie 79: 5-28.

One of the principal lacunae in our understanding of development in insects and other eucaryotes is that of cellular determination. How are different cells, all containing the same genetic information in their chromosomes, programmed for a specific fate during development? An answer to this question has awaited a fuller understanding of how genes work at the molecular level and the discovery of appropriate, eucaryote, experimental systems. Practitioners of the science of biochemical genetics have come a long way towards providing the first, while the imaginal discs of holometabolous insects seem to constitute the second.

Experimental imaginal disc research began when Ephrussi and Beadle developed a technique for transplanting discs dissected from donor larvae of *Drosophila* into larval or adult hosts by means of a micropipette. When a disc is transplanted into a larva of the same age as the donor, it develops synchronously with the host and undergoes metamorphosis within it. On emergence of the adult the implant can be removed and examined. In all experiments, the discs were found to differentiate *autotypically*, i.e. into the structure for which the disc was originally determined. Similar results were obtained with fragments of discs, indicating that each disc of the third (last) larval instar contains a mosaic of different cell groups, each determined to form a specific part of the adult structure.

One of the principal advantages of using *Drosophila* species in this work is the availability of a large number of genetic marker mutations. These can be easily recognized by their effect on imaginal surface structures exemplified by coloured, crooked, or multiple hairs, microtrichiae, and bristles.

Discs may be dissociated enzymatically or mechanically into small groups of cells or into single cells. If such cells from identical discs of different mutant donors are mixed together and injected into a wild-type host larva it is found, after metamorphosis, that the cells from different donors collaborate to form normal but mosaic adult structures. The contributions of individual cells to the development of the whole structure can be recognized because they differentiate into bristles and hairs having the colour and shape of the donor phenotype.

Evaluation of other experiments involving the mixture of mutant cells from dissociated discs of different kinds (e.g. wing and leg; haltere and eye-antenna) showed that a cell from

a given disc will only associate with other (*isotypic*) cells from the same kind of disc and not with those (*heterotypic* cells) from other kinds of discs. The association of isotypic cells and separation of heterotypic cells is considered by Gehring to be achieved by cell migration and selective adhesion of cells.

If imaginal discs are transplanted into the abdomens of adult flies rather than into larval hosts, they proliferate into blastemas. The host's haemolymph serves as a culture medium which allows proliferation but does not induce differentiation, probably because of the absence of ecdysone. Such blastemas can be cultured indefinitely by dissecting them from the host fly every two to four weeks, cutting them into fragments and injecting the fragments into fresh host flies. Other fragments are injected into host larvae where they undergo differentiation on metamorphosis of the host. These larval "test implants" provide information about the capacities of the cultured cells for differentiation. Using this technique, Hadorn and his students have shown that the cultured cells maintain their capacity for normal (autotypic) differentiation even after several years of culturing, i.e. they maintain their state of determination.

However, in cultured blastemas, occasional changes in cell heredity affecting determination occur. Some of the cells, when tested in larvae, at metamorphosis differentiate *allotypically* into organs *other* than those for which the cells were originally determined. For example, a fragment of genital disc blastema might differentiate into antennal or leg structures. This change in cell heredity is called *transdetermination*.

Using these culturing techniques Hadorn's group showed that for each state of determination in a particular disc, there exists a probability of transdetermination in a specific direction. Sometimes these changes in prospective fate are reversible, sometimes not. The only factor so far detected which influences the frequency of transdetermination is proliferation. This suggests that cell divisions are a necessary prerequisite for it.

Naturally-occurring developmental abnormalities leading to the same effect as transdetermination can be induced by homoeotic mutations. A common example is *aristapedia* in which the arista of the antenna is replaced by a tarsus. Gehring suggests that a single mutant "switch" gene could bring into action all the genes necessary for the differentiation of a leg disc in a blastema previously determined to form head structures. Some homoeotic mutations are temperature-sensitive. Temperature-sensitive alleles of the mutation ss^a, for example, cause parts of the antennal disc to develop into leg structures at 16°C and into antennal structures at 25°C with the temperature-sensitive period lying in the third-instar. Gehring suggests that the main problem for future research is the identification of the carrier of determination.

In cyclorrhaphous Diptera, the somatic cells exhibit pairing of homologous chromosomes similar to that occurring at synapsis during prophase I of meiotic cells. By treating prophase cells with X-rays it is possible to induce mitotic recombination in them. Strains of *Drosophila* are used which are heterozygous for a recessive marker gene. If a cell is irradiated just before it divides, crossing-over may be induced such that one or both of the daughter cells become homozygous with respect to the mutant gene. The clone of cells arising from this initial daughter cell will, with subsequent development, appear in the adult as a patch of mutant tissue surrounded by wild-type tissue.

Using this technique Schneiderman and García-Bellido and their students have shown that oriented cell divisions, differential mitotic rates, and local differences in cell size are all involved in producing changes in form in the discs during their development. They have also shown that determination is a gradual, progressively-narrowing phenomenon. By irradiating individual cells at different stages of development and then following what happens in the irradiated area, these workers have been able to determine the number of blastoderm cells

in the embryo that give rise to each imaginal disc and to prove that determination of adult structures begins during blastoderm formation.

Experiments using gynandromorph tissue can yield the same kind of information. Gynandromorph tissues are mosaic and contain both male and female cells. In *Drosophila* they arise when one of the two X-chromosomes is lost during development of a female embryo, resulting in female (xx) and male (xo) tissue patches. If the insect was originally heterozygous for x-linked cell marker mutations affecting bristle colour or shape, for example, the mosaic is recognizable on the body surface of the adult fly because the recessive mutations are uncovered through the loss of wild-type alleles. Though gynandromorphs are rare in nature, they can be induced artificially in various ways.

Studies of the ultrastructure of imaginal discs, as reviewed by Ursprung, have revealed no differences between cells of different discs. They have yielded evidence suggesting that the surface increase accompanying disc eversion in the pupal stage results largely from a change in shape of the epithelial cells comprising the disc; in larvae they are columnar; in pupae cuboidal. Some mutants of *Drosophila* lacking portions of or complete appendages in the adult have imaginal discs in which many cells die during development. Others have smaller than normal discs.

As emphasized by Fristrom and Oberlander, *Drosophila* imaginal discs are almost ideal material for studying the biochemical effects of hormones on differentiating tissues. They are easy to culture *in vitro* and their only disadvantage, their small size, has been overcome by the perfection of mass isolation techniques (up to 220,000 discs per day). Since synthetic juvenile hormone and ecdysones are commercially available, many breakthroughs in our understanding of the biochemistry of development are in the offing. Fristrom and his colleagues have found that β-ecdysone is much more active than α-ecdysone in inducing the synthesis of RNA, principally ribosomal, in cultured discs. Ecdysone apparently enters the disc cells where it directly affects transcription. No "second messenger" such as cyclic AMP which mediates the action of several different hormones in vertebrate systems has been found. Increased protein synthesis results from increased RNA synthesis and these proteins probably participate in the orientation, assembly, or function of microfibers evoking the change in cell shape causing appendage eversion during pupation. It was formerly thought that blood pressure was responsible for eversion *in vivo*, but discs evert just as successfully when removed and cultured *in vitro* with β-ecdysone. Juvenile hormone acts directly and antagonistically with ecdysone on both synthesis and eversion. Younger discs are less sensitive to both juvenile hormone and ecdysone than mature discs. If discs are cultured with fat body or in media conditioned with fat body, the effects of both juvenile hormone and moulting hormone are more rapid, suggesting that the fat body may influence the acquisition of competence by the disc.

Disc research has become a meeting ground for geneticists, developmental biologists, entomologists, biochemists and endocrinologists. Thus, this book deserves and will probably have a wide circulation. Although it is well produced, the book has several errors in typography and style ("prepupal" is usually spelled "prepual" and "for example" is always abbreviated whatever the context). Some contributors to the book (e.g. García-Bellido) presuppose more background on the part of their readers than do others (Gehring, Fristrom) and some (Fristrom) write more clearly. A detailed table of contents compensates in some measure for the lack of both author and subject indices.

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